THE NYMPHAL DEVELOPMENT FOR THE ROACH, PERIPLANETA AMERICANA L.*

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Now that the American roach, *Periplaneta americana,* is being widely used as an experimental animal in physiological and toxicological studies, it seems desirable to obtain a thorough understanding of its life history. This paper reports information which deals mainly with the duration and normal number of instars in the development of this species.

In 1917, Marlatt stated that little was known concerning the life history of the American roach. He reported that the nymphal development period for roaches from one egg case varied between 246 and 336 days. Laing (1921) described *P. americana* as one of the common roaches in Great Britain and stated that the nymphal period was supposed to be greater than one year in the United States, but that it had not been worked out in Britain. Later, von Fischer (1927) reported some of her own findings, and compared them with Fibiger's observations. Fibiger found that adulthood was reached in seven to eight months. However, von Fischer claimed that this was too long and that normally adulthood was attained in four and a half to five months, but that nymphal development might extend over a 15-month period. She was able to count 10 molts which were about 14 days apart.

Sein (1923) reported that American roaches in Puerto Rico needed about 350 days in which to become adults. Nigam (1923) noted from seven to nine molts for this species in India, and stated that the nymphal stages lasted for a period of from 300 to 600 days.

More recently, Gould and Deay (1938) found that the males of *Periplaneta americana* took about 20 days longer to reach adulthood than did the females, and that the developmental periods varied between 285 and 616 days with an average of 409 days. They believed that "the American roach apparently molts 13

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times'' and that the first three or four molts were approximately a month apart.

METHODS

Upon hatching, the first instar nymphs were isolated and placed at a constant temperature. Those which were studied to determine the number of molts were kept in cabinets in which the temperature varied within one degree of 29° C. The humidity was partially controlled by saturated NaCl solutions. These roaches were all descended from colonies which had been laboratory reared for several generations. The experimental animals were fed whole wheat bread, banana, and raw beef steak.

Groups of from 25 to 50 first instar roaches were placed in 250-cc. beakers, the tops of which were greased in order to prevent escape of the specimens. These roaches were then observed at daily intervals, or even more often, throughout their nymphal periods. When one molted, it was removed and placed in another container. In this manner, only those roaches which were in the same instar were caged in the same beaker. As the insects neared maturity, fewer and fewer individuals were kept in each container in order to prevent crowding. Thus, the number of days which intervened between hatching and a particular molt was recorded, and in turn, the average number of days per instar could be computed.

RESULTS AND DISCUSSION

It is an extremely difficult task to determine accurately the number of times that a cockroach molts. During the course of these investigations several morphological changes proved to be beneficial in identifying impending or recently completed molts. For several days prior to molting the nymphs appear to be quite slender. Immediately upon molting the roach is, of course, completely white with the exception of the eyes which are dark in color, but within a few hours the integument darkens and becomes light brown. For a day or two following the molt, the edges of the sclerites are darker than the centers and for several days the nymph is rather broad in contrast to its appearance prior to the molt. Cast skins are sometimes helpful, but cannot always be relied upon because they are readily eaten by the molted roach. Gould and Deay reported that in all but the last two instars the

cast skins were devoured. This was not observed in the present experimentation. Cast skins were usually not eaten by the second or third instar nymphs, but after the third instar, all or part of the exuviæ was eaten. Often fragments were helpful in the discovery of newly molted individuals.

The data from five representative groups of roaches observed during their entire developmental stages are listed in Table I. Several other groups were started, but were discarded before their entire nymphal periods were completed. As far as they went, the instar intervals noted for these latter groups were quite similar to those presented in Table I.

Since, as explained above, it was often difficult to determine accurately whether or not a roach had just molted, it was necessary to discard those roaches about which there was any question as to the proper instar. This elimination was an unfortunately necessary procedure, for even with daily or semi-daily observations, molts could not always be definitely noted. Especially was this true among the earlier instars when the developmental rate is more rapid. Therefore, as the experiment progressed, fewer and fewer individuals were retained, and a relatively small number of insects remained by the time adulthood was reached. Only those roaches which became female adults at the completion of the eleventh instar, or male adults upon the completion of the twelfth instar, are included in Table I for those stages beyond the ninth instar. Reasons for this selection are discussed in a later paragraph.

Several facts and trends are readily noted in Table I. The number of individuals decreased throughout the experiment. This is partially explained by the fact that some roaches were discarded. However, there also was a relatively high death rate which could not be adequately explained. Even in stock cages a large number of nymphs fail to reach maturity. It may be that this high developmental mortality is a normal phenomenon of the American roach. Although there is considerable variation between groups, the duration of the early instars averaged less than three weeks. This period was gradually increased with advancing age until the tenth, eleventh, and twelfth stadia averaged more than 30 days. In general, females required 11 instars in

TABLE I

THE DURATION OF INSTARS FOR FIVE REPRESENTATIVE GROUPS OF ROACHES

Molt	A			B			C			D			E			Summary all groups		
	No. ind.	Av. days since hatch	Av. days between molts	No. ind.	Av. days since hatch	Av. days between molts	No. ind.	Av. days since hatch	Av. days between molts	No. ind.	Av. days since hatch	Av. days between molts	No. ind.	Av. days since hatch	Av. days between molts	Total No. ind.	Av. days since hatch	Av. days between molts
1	36	11	11	35	12	12	28	25	25	52	19	19	34	19	19	185	17	17
2	30	25	14	32	32	20	21	50	25	41	35	16	32	35	16	156	35	18
3	28	39	14	29	50	18	21	65	15	39	52	17	30	57	22	147	53	17
4	24	56	17	29	69	19	20	94	29	38	76	24	17	75	18	128	74	21
5	22	74	18	19	89	20	18	114	20	24	102	26	16	97	22	99	65	21
6	18	96	22	16	113	24	15	125	9	13	122	20	15	124	27	77	116	20
7	14	119	23	16	134	21	14	151	26	8	142	20	11	139	15	63	137	21
8	10	143	24	7	139	5	13	180	29	9	180	38	7	179	40	46	164	27
9	7	164	21	7	171	32	10	206	26	10	206	26	7	193	14	41	188	24
10	7	198	35	3	200	29	3	239	33	2	240	34	5	226	33	20	221	33
♀ adult	0	.....	.....	1	240	40	3	265	26	2	268	28	3	253	27	9	256	30
11	6	231	33	2	241	41	0	.....	.....	0	.....	.....	2	271	45	10	248	40
♂ adult	6	267	36	2	275	34	0	.....	.....	0	.....	.....	2	328	57	10	290	42

which to complete their development, while males passed through 12 stages.

There were instances in which the number of molts needed for the roaches to become adults was different from that in Table I. However, there is some evidence that 11 and 12 represent the number of instars which females and males, respectively, generally need to complete their development. Support for this conclusion is offered in the following data.

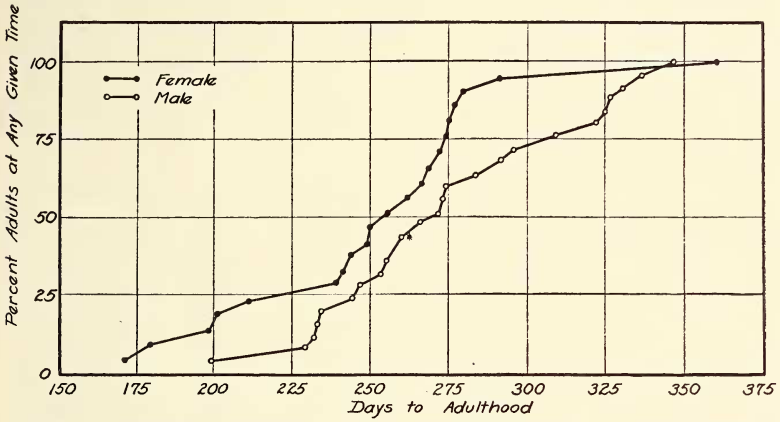

Fig. 1. The rate at which 46 roaches reached maturity. * This represents the emergence of two individuals. All other dots indicate the emergence of one roach and also show the per cent of males or females which have reached adulthood at that given time.

In Figure 1 the rate and time of adult ecdysis for 25 males and 21 females are shown graphically. The first female passed into the adult stage 27 days prior to the emergence of the first male. Also, a female was the last to become an adult. However, there was only one female as opposed to seven males which reached adulthood after more than 300 days. The graph indicates that the females tended to emerge about 25 days earlier than the males. When the emergence dates were averaged, the time was found to be 251 days for the females and 276 days for the males.

Similar results were obtained under different conditions. Several groups of roaches, totaling 62 individuals, were started at 35° C. and later it became necessary to place them at a temperature of 29° C. Approximately half of their nymphal period was

spent at each temperature. For this group, the developmental period averaged 227 days for 11 females (range: 180–411) and 252 days for 10 males (range: 190–367). In a dietary study (unpublished) the authors have found that for 81 male roaches the nymphal period on four different diets averaged 48, 61, 49, and 17 days longer than that for 76 females on the same respective diets. These experiments were performed at room temperature, and the average time for adult emergence was about 365 days which agrees with the work of other investigators. As stated above, Gould and Deay also observed that females became adults in a shorter time than did males. This time difference between the sexes, with a longer nymphal period for males, can be accounted for by longer intervals between molts, or by one or more additional instars.

The facts seem to indicate that the male roach generally requires an extra instar to reach maturity. For 19 males which were reared at 29° C. and whose molts were carefully checked, 10 or 53 per cent became adults upon the completion of their twelfth instar. Six reached adulthood after 11, two after 13, and one after 14 stadia. For 15 females, 12 or 71 per cent became mature after 11 instars, two after 12, and one after 13. Approximately two-thirds of the insects started at 35° C. and then shifted to 29° C. attained maturity after 11 and 12 instars for the females and males, respectively. Therefore, it appears that usually the male needs an additional instar in order to become adult.

The number of molts reported in this paper is not in agreement with that noted by von Fischer, Nigam, or Gould and Deay. Nigam and von Fischer are quite positive in their statements concerning the number of molts, namely seven to nine, and ten, respectively. Gould and Deay were unable to ascertain definitely the exact number, although they report about 13 molts. The period for nymphal development reported by them is similar to that noted for room temperature in the present account. As has been suggested by Griffiths and Tauber (1942), it is entirely possible for an insect which is as universal in distribution as is the American roach, to have developed biological races in many localities of the world. Also, nutritional and temperature changes may markedly affect the developmental period. Thus, it

is to be expected that discrepancies may appear when studies are carried on in widely separated geographical areas, or under different environmental and experimental conditions.

Although no positive explanation can be offered at this time for the increased number of instars required by some individuals of both sexes, some suggestions can be made. Seamans and Woodruff (1939) stated that for the German roach, *Blatella germanica,* the number of molts could be increased by a deficient diet or by bodily injury, such as the loss of an appendage. It would seem entirely probable, therefore, that if in some manner conditions were not altogether satisfactory, the nymphal stadia for certain individuals might be increased above the normal. This is probably a partial explanation for some of the variations in the number of molts in the present experimentation. Although experimental diets may seem adequate, they are often restricted and monotonous. Autotomy, also, might be a contributing factor, for, in isolating and transferring newly molted specimens, forceps were sometimes necessary to secure a lively individual. If too much struggling occurred, a leg was detached.

Another factor which seems to contribute to longer nymphal periods was noted when an attempt was made to rear isolated nymphs at room temperature. Twenty-five newly hatched nymphs were placed in individual 250-cc. containers. They were fed mixtures of Pablum, banana, whole wheat bread, and beef steak. As this is written more than 600 days have elapsed since these observations were started. Only two individuals have reached adulthood. One, a female, completed her final molt after 332 days; the other, a male, after 573 days. Both passed through 12 nymphal instars. Of the other 23, only two are still alive and the most nearly mature of these is a male. Thus, it appears that the American roach does not thrive when an individual is isolated and that several roaches must be together in order for optimum development to occur. Neither a satisfactory explanation nor the optimum number of roaches can be presented at this time, but it seems possible that this isolation or "under-crowding effect (Park, 1941) may be related to similar results recorded by Chapman (1928), Eigenbrodt (1925), and Pearl (1927, 1932). Eigenbrodt stated that for *Drosophila* the largest individuals were ob-

tained in vials which had a population density of eight to 16 larvæ. Pearl, Miner, and Parker (1927) found that 30 to 50 *Drosophila* per bottle proved to be optimum when longevity was used as a criterion. Chapman (1928) and Pearl (1932), working with *Tribolium* and *Drosophila,* respectively, reported that two pairs of adults per unit volume produced more offspring than did insects at either higher or lower densities.

Regeneration was found to be a relatively common phenomenon. Replacement of tarsal joints, the tarsi and the tibia, cerci, and antennal segments was observed to take place with a single molt intervening between the loss and the regrowth of the appendage. Regeneration is apparently impossible for the adult roach.

Gould and Deay have described a method for determining the sex of immature roaches which is based upon a morphological difference in the sternite of the ninth abdominal segment rather than upon sub-anal stylets. This method has been used by the authors and is quite satisfactory. Subanal stylets are present in both sexes until the late instars, when they appear to be lost in the female nymphs. In the present work, it was noted for the females with 11 molts that the sub-anal stylets usually appeared to be very small in the tenth instar and that they seemed to disappear in the eleventh instar. In the male, they persist through the entire life span.

No definite means for the determination of individuals in a certain instar has been found, but since both the antennæ and the cerci have an increased number of segments with each successive molt, it is entirely possible that a method can be worked out by which the various stadia can be recognized. The last instar is readily identified by the well developed wing pads.

By using data previously reported by Griffiths and Tauber (1942), it is possible to arrive at a comparatively accurate figure for the total life span of the American roach, *Periplaneta americana,* as it exists under laboratory conditions in Iowa. Foods fed to these laboratory-reared specimens seem to have constituted an adequate diet. At room temperature subject to seasonal and diurnal fluctuations, the data in Table II have accumulated.

Fluctuating temperatures during the winter months, with less

heat in the laboratory outside of class hours unquestionably prolongs the developmental period. Natural variations in the length of the nymphal stage plus possible contributing environmental factors generally carry the immature stages along for from nine to 13 months, or even longer. A complete reproductive cycle could possibly occur within a minimum of 243 days (35 + 199 + 9), but would probably average about 434 days (53 + 365 + 16). Also, it could take as long as 573 days (72 + 465 + 36).

TABLE II

Normal Extent of Various Phases in the Life Span of the American Roach

Incubation of eggs (days)	Nymphal development (days)	Preoviposition period (days)	Adulthood (days)*		
			♀	♂	♀ & ♂
Range 35–72*	199–465†	9–36*	90‡–706	90–362	90–706
Avg. 52.7*	365†	15.6*	225	200	213

* Data from Griffiths and Tauber (1942).

† These figures have been determined from specimens fed on what is believed to be an adequate mixture. Roaches on inadequate diets may take from two to three years or longer in order to complete their development. (Experiment in progress.)

‡ This minimum was arbitrarily selected for both males and females by discarding those individuals which died within 90 days after the final molt. Such a selection was made to assure the observation of healthy, uninjured specimens.

The entire life span from egg to the "natural" death of a presumably healthy adult might cover a minimum of 324 days (35 + 199 + 90). An average life span would probably be about 631 days (53 + 365 + 213). However, if an individual roach enjoyed maximum longevity, the life span could be about 1243 days (72 + 465 + 706).

CONCLUSIONS

All conclusions are concerned with the American cockroach, *Periplaneta americana* L.

1. At 29° C., the female roach generally requires 11 and the male 12 instars before reaching adulthood. More stadia are necessary for some individuals. It is suggested that this increase

may be due to unfavorable environmental conditions or bodily injury.

2. The males averaged 276 (range: 198–346) and the females 251 days (range: 171–360) to complete their development at 29° C. Similarly, at room temperature the females became adults sooner than did the males.

3. Under laboratory conditions and at room temperature, a complete reproductive cycle ("egg to egg") may be passed in about 243 days, but normally it takes about 15 months. The entire life span (egg to "natural" death) usually extends over a period of about 630 days, but may last for more than 1,200 days.

4. The regeneration of certain parts such as portions of lost appendages is possible throughout nymphal development.

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